SHORTER ARTICLES AND DISCUSSION

HYBRIDIZATION AND EVOLUTION

SOME years ago the writer made a cross between the two species *Nicotiana rustica* L. and *Nicotiana paniculata* L.[1] Since the hybrids obtained through this mating are not completely sterile, some biologists may perhaps maintain they are not distinct species, but such a claim is wholly arbitrary. In a sense, a species is a human concept and as such its definition may be carried to any ridiculous extreme, yet there is no more striking biological fact than that *in general* the great groups of living things do fall into specific subdivisions which many criteria show to be distinct, discontinuous, without intermediates. In two such groups fall the above types. Though their ranges overlap, they differ from each other in leaf, stem, flower and habit of growth much more than do several other pairs of species within the same genus between which hybridization is impossible, or where the hybrid is sterile.

The cross between these two species gives an F_1 generation intermediate between the two parents, and as uniform in each character as either parental group.

Few of the male or the female gametes are viable, yet by careful attention to pollination, from one to twenty seeds can be obtained in the capsules, where normally two hundred to three hundred seeds are found. These seeds produce an F_2 generation which is inordinately variable. No two plants are similar, and numerous types can be picked out which if found in the wild would undoubtedly be classed as different species. In genetic terms, the behavior of the two species may be described as follows: They differ in an extremely large number of inherited factors; and owing to these numerous differences, many of the otherwise possible combinations of F_1 gametes, are not functional. A huge percentage of expected combinations of both gametes and zygotes are thus eliminated.

The factors which in combination produce normal fertility,

[1] A detailed account of the genetic facts found in this study, has not yet appeared. A preliminary paper was published in the *Proc. Amer. Phil. Soc.*, 54: 70–72, 1915.

recombine in the Mendelian sense, quite as do the factors controlling the form of leaf and flower. The result is that after a few generations of selection one may obtain a variety of strains, uniform within each line, so fertile as to yield capsules with over ninety per cent. of the normal quota of seed, and so different from one another that the extreme types are more unlike than the two original species used in the cross.

After three years of selection (F_5), eight such strains remained out of a large series of selections studied earlier. It seems hardly necessary to describe the differences they exhibited. Suffice it to say that the smallest type was about 20 cm. in height with small smooth oval leaves, and the largest was nearly 200 cm. in height with wrinkled cordate leaves some of which were 50 cm. in length.

These eight strains were crossed in all possible combinations, and every F_1 generation exhibited as high a degree of fertility as that shown by the parents.

To the writer it seems possible that these results have a bearing on certain theoretical problems which may not be clear at first sight.

A few years ago Lotsy[2] published an extended paper based on a very limited number of crosses in the genera *Nicotiana, Pisum, Petunia* and *Antirrhinum,* where partially sterile F_1 plants produced exceedingly variable progeny,—results wholly comparable with our own. From these observations, neglecting all evidence of the appearance of mutations in controlled pure lines, Lotsy founded a theory of evolution. His arguments were based upon five assumptions: (1) that all characters obey the Mendelian law of heredity, (2) that acquired characters are never transmitted, (3) that homozygotes are absolutely constant in succeeding generations, (4) that there has been no proof of variation independent of crossing, and (5) that the variations observed after crossing are sufficient to account for evolution.

Naturally numerous criticisms can be made against this extreme interpretation. One need only inquire as to the source of the original variations which are to form the basis of all Mendelian recombinations, to show the untenability of the position. On the other hand, it will be admitted by all that hybridization has played some part in evolution, and it is of some importance to endeavor to determine the limits of its rôle.

[2] Lotsy, J. P., "La théorie du croisement," *Arch. Néerland. Sci. Exact. et Nat.,* III, B, 2: 1–61, 1914.

The observations of the writer on the enormous variability of the F_2 generations arising from partially sterile F_1 generations produced by crossing species, led him to suspect that such combinations might be the basis of a great deal of variability responsible for evolution under domestication. A careful survey of the evidence relating to the origin of modern horses, cattle, sheep, swine, dogs, guinea pigs, fowls, ducks, and geese on the one hand, and varieties of wheat, corn, barley, oats, rye, apples, grapes, roses and begonias on the other hand, shows that in every case several related wild or semi-wild species exist which will cross together and yield partially fertile offspring. Doubtless many other species which have shown great improvement under domestication, would be found to have wild relatives which behave similarly, should they be investigated. Both the historical and the experimental evidence, therefore, point to hybridization, and particularly to species of hybridization, as the great single cause of evolution under domestication.

At the same time, one must not confuse evolution under domestication with natural evolution. The outstanding biological feature characteristic of the varied groups of domestic animals and of cultivated plants, is the perfect fertility within each group. A marked peculiarity of the great majority of natural species is their sterility with one another, the origin of which has long been a stumbling block to writers on evolutionary biology. Our own experimental evidence, as far as it goes, and observations on domestic forms which presumably have originated from combinations of two or more wild species, yield not the slightest indication of a tendency toward the production of segregates that exhibit either incompatibility in crosses or sterility of the individuals produced by hybridization.

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THE MEASUREMENT OF LINKAGE

LINKAGE is a name for that tendency sometimes shown by genes to maintain in hereditary transmission their previous relations to each other. Thus if two linked genes, A and B, enter a cross together, in the same gamete, they will oftener than not be found together in the gametes formed by the cross-bred individual. And if the same two genes enter the cross separately,